A study of moorland invertebrates and a comparison in the relative effectiveness of new and old pitfall traps used for sampling

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A study of moorland invertebrates and a comparison in the relative effectiveness of new and old pitfall traps used for sampling

by

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SUMMARY

1. Invertebrate sampling using pitfall traps at 14 sites on Chapel Fell from 1 April to 8 July, revealed invertebrate totals between sites to be significantly different.

2. These differences were not found to be correlated to soil moisture content that was recorded on 22 July of 1994, but it is suggested that low totals occurred in habitats more prone to losing moisture in dry weather, and at these locations, dessication may have caused mortality in small young invertebrates.

3. Tipulid totals were found to differ significantly amongst sites, and in most areas had increased in number compared to 1992 and 1993 site totals.

4. The large overall increase of tipulid totals on Chapel Fell in 1994 compared to 1993, was largely due to the abundance of *Tipula subnodicornis*. The increase of this, and other species, is attributed to sufficiently wet conditions during the early stages of the lifecycle in 1993.

5. Abundance of *Tipula subnodicornis* was found to be higher at some sites than others. Its proportional increase at individual sites between 1993 and 1994, also varied between sites, and was found to be greater in peat areas where in 1993 there had not been many *Tipula subnodicornis* present. Density-dependence is suggested to be the cause of this phenomenon.

6. Tipulid emergence began later in May of 1994, than in May of 1993, but peak abundances coincided, in early June of each year. In 1992, however, peak abundance was recorded a fortnight earlier than it was in 1994. The delay in emergence in 1994 was attributed to the late arrival of warm spring weather.

7. New pitfall traps that were used for sampling were found to capture more invertebrates than old pitfall traps that had been in use for a number of years. Differences between numbers caught in each, however, decreased with time and this was attributed to an external influence, probably related to seasonal change.

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1.0 INTRODUCTION

Studies on this site started as part of an invertebrate monitoring project on top of Chapel Fell, a moorland ridge in the Pennines. This study was originally commissioned by the Central Electricity Generating Board in 1989 as an environmental assessment, but since then, the monitoring of various invertebrate groups has been continued each year. One particular family of insects that have been studied closely are the Craneflies (Tipulidae, Diptera), and in this study their numbers, distribution and emergence times on Chapel Fell were examined for 1994 and compared with data from previous years.

Twelve sites were originally chosen for invertebrate sampling on Chapel Fell, on account of their differing soil/vegetational characteristics and site structure. These sites represent a variety of mineral and peat soil habitats, and have been described in a previous invertebrate study by Coulson and Goodyear (1989). This information has been utilised in this study, together with soil moisture data gathered at the end of monitoring for this project in July 1994.

Tipulids are important to the moorland ecosystem as, at certain times of the year, they provide a major food source for insect-feeding animals such as the Common frog (*Rana temporaria)*, Pygmy shrews (*Sorex minutus*), and birds such as Meadow pipit (*Anthus pratensis*) and waders (Coulson,1988). Tipulids in turn, during their larval stages, are consumers of moorland vegetation and are considered the main herbivore after sheep (Coulson & Whittaker, 1978).

In this study, tipulids were identified to species level and and an attempt was made to relate the results obtained through pitfall trapping to the local habitat they were predominantly found in. Using data from previous years it was possible to examine changes that had occurred in tipulid numbers, site by site. This was done with particular reference to the most common tipulid species - *Tipula subnodicornis.*

The pitfall traps traditionally used for this work are plastic screw-top containers which can be sealed, and are both durable and convenient to carry in the field due to their light weight. At the start of monitoring in 1994, however, some of these traps were nearing the end of their life, and so it was decided to replace them with new ones. To ensure against this action being a variable factor in the monitoring method, only half of the traps were replaced and the positions of old and new were alternated fortnightly when trap collection took place.

Differences that may have occurred in their effectiveness to trap invertebrates were investigated by examining numbers of organisms entering the two types of traps. Trap efficiency relating to factors such as size and design has been discussed by Greenslade (1964) and Luff (1975); and in addition, this study draws attention towards considering trap age.

This study took place over three months (from mid-April to mid-July), involving seven fortnightly collections of pitfall traps. Traps were collected and at the same time replaced with the traps for the following period of sampling.

2.0 METHOD

2.1 The study area

Chapel Fell (NY 863349) is a moorland ridge situated on the eastern edge of the northern Pennines. The ridge summit is at an altitude of 703m (the altitude of the sites looked at in this study, ranged between 550 - 650m). The climate for the area is likely to be the same as that recorded at Moor House National Nature Reserve, which, on a clear day, is within visual distance. This upland moorland receives *c* 1900mm yr^{-1} of rainfall, occurring on an average of 250 days, and has a mean temperature of >5.6^{o}C which confines the growing season to about 180 days from May to October (Heal & Smith, 1978). These climatic features provide the conditions needed for the formation of peat soil, with the breakdown of organic material proceeding only slowly.

Where rainfall exceeds 1000mm, and warmest temperatures are less than 15 ^{o}C (Lindsay *et al.*, 1988), blanket bog is able to develop in areas of poor drainage, with associated vegetation such as *Eriophorum angustifolium*, *Calluna vulgaris* and *Sphagnum* spp.. A cool wet climate as described, is essential for sustaining waterlogged conditions, and occurs in upland and northern areas of Britain. Chapel Fell is one such example where these conditions prevail, but due to the alternating, underlying geology and slope of the land, other soil types can also develop. Thus, in certain intermittent areas of limestone where drainage is good, mineral grassland is present.

This particular monitoring study upon Chapel Fell commenced in 1989, when 12 sites (A-M, not inclusive of I) were chosen for sampling on account of their differing soil and vegetational characteristics. A further two hag sites (N,P) were added in 1991 to confirm the accuracy of data obtained from a similar hag site (H).

The vegetational and soil characteristics of the study areas listed below, are as according to Coulson and Goodyear (1989). To this information has been added data on soil moisture content recorded on 22 July 1994.

Data on soil moisture content was obtained by first collecting soil cores with a corer, from the top 5cm of soil at each site (A-M). Three cores were taken from each site, at regular intervals along the transect, to take into account any local variation in levels of soil moisture that may occur along the transect length, and the average of readings taken from these were recorded for each site. The soil cores were processed in a laboratory by weighing them on electronic scales before placing them in an oven for 48h at 105 °C to evaporate the water. After this they were re-weighed, placed in an oven for a further 12h, and and weighed once more, to ensure that they had reached constant weight and thus were fully dehydrated.

2.2 Site descriptions

The following information relating to soil organic matter and vegetation, was recorded in 1989 and is expected not to have changed much since then. Soil moisture readings, however, tend to vary more with time and thus were taken at the end of this study in 1994.

Site A.
Soil moisture content: 58%
Soil organic matter content: 27%
Soil type: Well drained mineral
Dominant vegetation: Grasses, *Juncus squarrosus* (25% cover)
Common grasses: *Agrostis tenuis, Anthoxanthum odoratum, Deschampsia flexuosa, Festuca ovina*
Abundant herb: *Galium saxatile*

Site B.
Soil moisture content: 87%
Soil organic matter content: 99%
Soil type: Deep peat
Dominant plant: *Eriophorum vaginatum*
Common plant: *Vaccinium myrtillus*
Common grass: *Deschampsia flexuosa*

Site C.
Soil moisture content: 49%
Soil organic matter content: 33%
Soil type: Mineral alluvial - five metre wide strip adjacent to a stream
Dominant vegetation: Grasses - *Nardus stricta* and *Deschampsia flexuosa*
Common vegetation: *Anthoxanthum odoratum* and *Festuca ovina*
Less common: *Juncus effusus* - in nearby clumps

Site D.

Soil moisture content: 84%

Soil organic matter content: 89%

Soil type: Shallow peat

Dominant vegetation: *Eriophorum vaginatum, Deschampsia flexuosa*

Common vegetation: *Vaccinium myrtillus, Vaccinium vitis-idaea, Empetrum nigrum* and *Eriophorum angustifolium* - in interspersed hummocks

Site E.

Soil moisture content: 82%

Soil organic matter content: 97%

Soil type: Blanket bog - level site with small exposed peaty pools.

Dominant plant: *Eriophorum vaginatum*

Common plant: *Calluna vulgaris* (30% cover)

Site F.

Soil moisture content: 48%

Soil organic matter content: 44%

Soil type: Alluvial grassland -five metre wide strip alongside a stream adjacent to blanket bog

Dominant plant: *Nardus stricta*

Within a few metres from the traps and away from the stream, transition to (*Nardus)* grassland occurred, with *Vaccinium myrtillus*, *Calluna vulgaris* and *Eriophorum vaginatum* co-dominant before giving way to the *Calluna vulgaris* dominated community on blanket peat.

Site G.

Soil moisture content: 83%

Soil organic matter content: 96%

Soil type: Blanket peat - with *Eriophorum* and ericaceous species abundant

Dominant vegetation: *Eriophorum vaginatum* and *Calluna vulgaris*

Common vegetation: Grass - *Deschampsia flexuosa* (21% cover)

Site H.
Soil moisture content: 84%
Soil organic matter content: 97%
Soil type: Peat - level site eroded to form hags and islands of vegetation
Dominant plant: *Calluna vulgaris*
Common vegetation: Cotton grasses - *Eriophorum vaginatum* and *Eriophorum angustifolium*

Site J.
Soil moisture content: 85%
Soil organic matter content: 99%
Soil type: Peat
Dominant plant: *Eriophorum vaginatum* hummocks alternating with wetter sparsely vegetated hollows containing *Eriophorum angustifolium,* and *Narthecium ossifragum.*

Site K.
Soil moisture content: 86%
Soil organic matter content: 99%
Soil type: Peat - similar to site B.
Dominant vegetation: *Eriophorum vaginatum,* and *Deschampsia flexuosa* co-dominant
Common plant: *Eriophorum angustifolium* (19% cover)

Site L.
Soil moisture content: 59%
Soil organic matter content: 61%
Soil type: Mineral grassland with a relatively high organic content.
Dominant vegetation: Grasses - *Festuca ovina,* and *Nardus stricta* in alternating tussocks.
Common vegetation: *Galium saxatile* (18% cover) and *Juncus squarrosus* (13% cover)

Site M.
Soil moisture content: 82%
Soil organic matter content: 98%
Soil type: Peat
Dominant vegetation: *Juncus squarrosus* (48% cover)
Common vegetation: *Deschampia. flexuosa, Festuca ovina* and *Eriophorum vaginatum*; interspersed amongst the *Juncus squarrosus.*

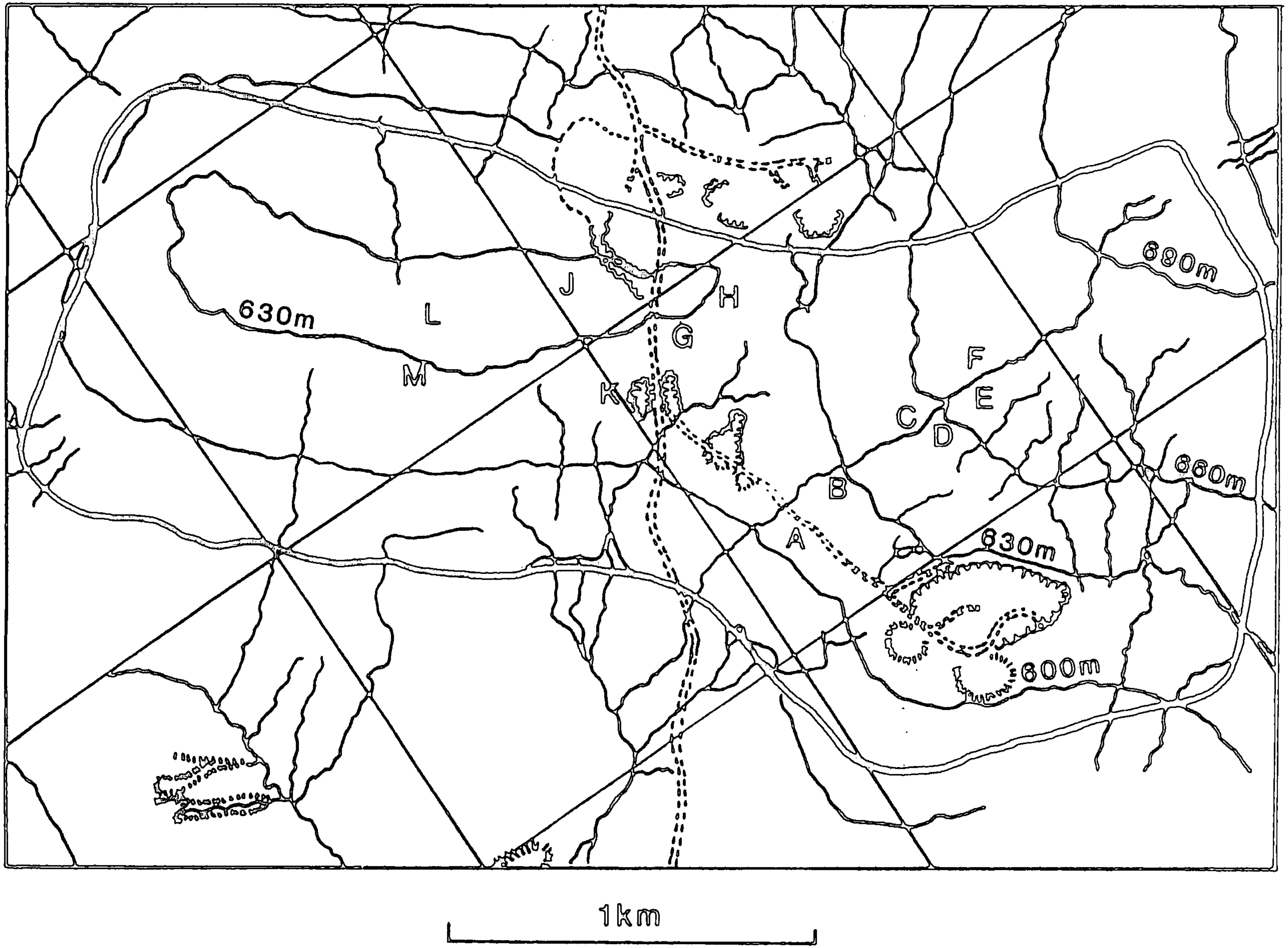
The sites can be broadly grouped into comparative field classes according to their soil and vegetational characteristics:-

Mineral limestone sites: A,C,F,L
These have a relatively low soil organic matter content and subsequently less water holding capacity. Accordingly, the soil mineral content is higher and this is reflected by the grasses present that typify such areas.

Peat:
B,D,J,K (Wet)
E,G,M (Dry)
H,N,P (Dry hag)
These sites have a high soil organic matter content and subsequently more water holding capacity than mineral (Crump, 1913). Other factors such as drainage will also affect the amount of water that is present and so peat sites have in previous studies, been divided up into wet and dry, according to their soil moisture content. In this study a third category was made for hag sites, which included site H, a site that before had been included with dry peat sites. Due to heavy rainfall that had occurred recently before 22 July, when soil moisture readings were taken, differences in water content between the peat sites were very small.

The sampling sites on Chapel Fell are shown on Map 1.

Map 1. Chapel Fell study area



2.3 Sampling procedure

Pitfall traps were collected and replaced fortnightly at 14 sites on top of Chapel Fell. The first traps were put out on 1 April 1994 and collected on 15 April 1994. In total, seven collections took place, with the final collection on 8 July 1994.

At each site 10 traps were placed at 2m intervals, alternating old and new along the transect. The positions of old and new traps were in turn alternated each fortnight to allow for variations relating to exact position of the traps within their microhabitat. In this way any difference in captures would be a feature of the trap types, rather than their individual locations. Traps were placed in the ground so that the mouth rim was level with the ground surface. Care was taken also, to ensure that there was no gap between the mouth rim and surrounding soil.

Each trap contained approximately 3cm of 2% formalin solution with a few drops of detergent in order to breakdown the surface tension, facilitating more effective trapping and preservation of fallen insects.

The traps used for sampling were made of plastic and had the following dimensions:

Mouth diameter:	Plastic thickness:	Trap height:	Overhang*:
Old: 47mm	1mm	127mm	6mm
New: 48.5mm	2mm	113mm	8mm

*Overhang; relates to the difference between the width of trap neck (mouth diameter + plastic thickness) and the trap's main body width.

Differences between traps were observed as follows:

1. Colour; New traps were an opaque white, while old pots were more translucent, and dull through the deposition of soil over time.
2. Smell; New traps had a plastic aroma.
3. Texture; Smoothness of surface in new traps was not as apparent in old, which, through the course of time had roughened due to dirt and wear.

After the traps had been in place for two weeks, they were collected and replaced by the next replacement set of traps. Sorting took place before the next collection two weeks later.

Invertebrates were sorted into their taxonomic groups and tipulid adults were further identified to species, using a light microscope and consulting a taxonomic key to the Diptera (Coe, Freeman & Mattingly, 1950). Use was also made of known-species reference samples, to compare with specimens caught during this study. Other invertebrates were identified to just their groups using a general taxonomic key to major British groups (Tilling, 1987). Specimens were stored in 70% alcohol in glass or plastic tubes.

The data obtained were processed using analysis of variance (ANOVA). As ANOVA is a parametric test, and counts of invertebrates are not usually normally distributed, the raw data were first transformed to a log scale to normalise them. When the number of traps used in each transect to investigate trap efficiency was the same as the number involved to investigate invertebrate habitat distribution (i.e. 10), two-way, with replication, ANOVA was used, with new or old traps as replicates of each treatment. On the last two occasions of sampling however (24 June, and 8 July), less than ten traps per transect were used in the trap efficiency part of the experiment, and so, separate one-way ANOVAs were carried out on the data, hence the variations given for the degrees of freedom.

3.0 RESULTS

3.1 Invertebrate distribution

The data obtained from Chapel Fell through fortnightly sampling at each of the fourteen sites were summed and compared for those areas to see if any differences in invertebrate population size occurred between habitats. Invertebrates overall did not correspond in any directly ascertainable way to soil moisture readings recorded in July (see Method) and neither were their significant differences between numbers ($F_{(2,9)}0.37; P>0.05$) within the broad site categories of:- mineral, wet peat, or dry peat as given for the area by Coulson & Goodyear (1989).

There were, however, obvious differences between individual sites and this variation was most apparent amongst the peat sites (Fig. 1), while mineral sites were more homogeneous for numbers of invertebrates.

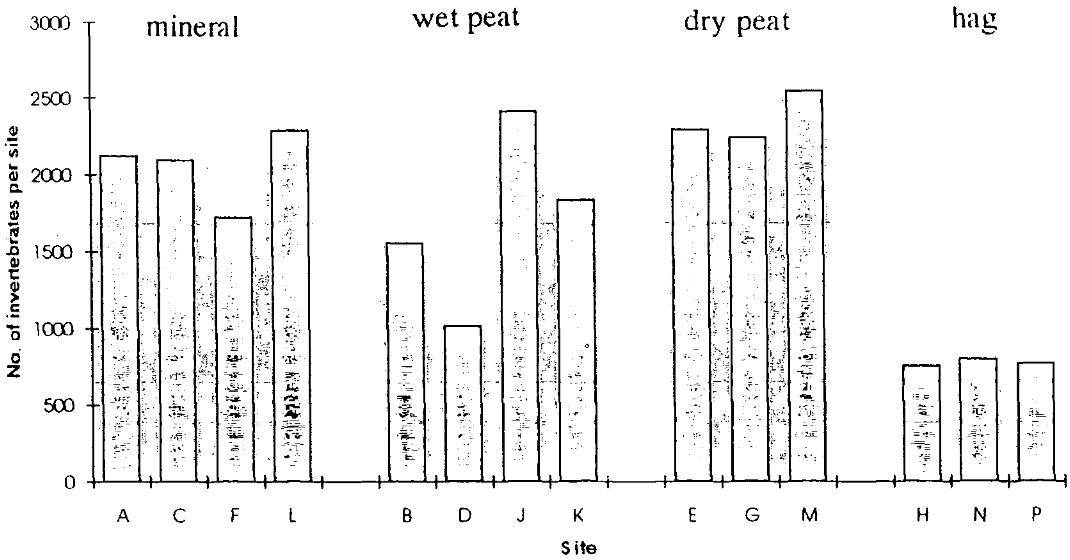


Fig. 1. Distribution of numbers of invertebrates (other than tipulids) captured in 10 pitfall traps at each site on Chapel Fell between 1 April and 8 July, 1994.

Site M, yielded high numbers of invertebrates - especially tipulids during their emergence in late May (Fig. 2), while sites H, N and P, featured relatively few invertebrates. Thus, within the range of peat sites, were encountered the highest and lowest number of tipulids and other invertebrates overall. This wide variation between sites cannot be accounted for by soil moisture readings that were taken from peat sites in July, as these were within 5% of each other. For this reason, the terms 'dry' and 'wet' peat given in previous studies are adhered to here only in a loose sense, and do not reflect site conditions in mid July, 1994.

Coefficient of variance (C of V) was calculated for invertebrate totals from the different sites, in order to see the magnitude of variation from the mean for each site. This necessitated, dividing the standard deviation of each site from the mean total for all sites, by the mean total itself. Results for this established highest variation in numbers of invertebrates between sites within the wet peat category (C of V = 0.34). This was followed by mineral (C of V = 0.12), then dry peat (C of V = 0.07), and lastly the hag sites which had the least numbers of invertebrates and lowest variance (C of V = 0.03).

Analyses of variance were executed on the invertebrate distribution data to determine the significance of the differences in numbers found between all sites. On the first date of sampling (15 April) there were significant differences in total invertebrate numbers between sites ($F=_{(13,112)}2.1;P<0.05$). From then on, differences between sites became highly significant with orders of significance showing a general trend of increase up until 24 June ($F=_{(13,126)}30.69;P<0.01$), and declining again thereafter ($F=_{(13,126)}12.66;P<0.01$). To investigate further the extent of unequal site distribution amongst invertebrates, some of the more commonly occuring invertebrate groups were examined. An analysis of variance revealed significant values to the pattern of unequal distribution amongst the sampling sites over the months of study for all of these groups. The results are given in Table 1.

For most invertebrate groups looked at, especially Araneae which reached a maximum significance value of ($F=_{(13,126)}15.9;P<0.01$) for distributional heterogeneity amongst sites on 24 June, the pattern in changes for magnitude of significance from April to July, followed a similar course as for total invertebrates. Coleoptera larvae, however, fluctuated in their significance (between $P>0.05$ and $P<0.01$) for distributional heterogeneity amongst sites throughout the study, while heterogeneity in staphylinids became increasingly significant from April through to July, except in the fortnight before 27 May when numbers suddenly dipped. Contrary to the general pattern of increasing numbers and significance in uneveness of distribution up until 10 June, numbers of Diptera larvae decreased from 15 April to 27 May, but then increased with a rise in significance for distributional heterogeneity amongst sites, till the end of sampling in July;

($F=_{(13,126)}8.1$;$P<0.01$). This decrease may, perhaps, be explained by - final larval instars entering pupation; and the increase by - the hatching of eggs giving rise to first larval instars, although the timing of this increase is dubious for this to be the explanation, as first larval instars of e.g. *Tiplua subnodicornis* are unlikely to have occurred in pitfall traps this early.

Table 1. Numbers of invertebrates trapped each fortnight, and the significance of heterogeneity in their distribution between sites on Chapel Fell during April to July, 1994.

Collection date	*15 Apr*	*28 Apr*	*13 May*	*27 May*	*10 Jun*	*24 Jun*	*8 July*
TIPULIDS	*absent*	*absent*	*absent*	*116* +	*6105* ++	*1347* ++	*175* ++
OTHER DIPTERA	*33* +	*171* ++	*461* ++	*1079* ++	*2969* ++	*1075* ++	*831* ++
DIPTERA LARVAE	*132* ++	*118* ++	*39* ++	*26* +	*38* ++	*55* ++	*79* ++
ARANEAE	*159*	*831* ++	*567* ++	*740* ++	*1852* ++	*3455* ++	*1701* ++
CARABIDS	*8*	*140* +	*342* ++	*224* ++	*580* ++	*573* ++	*852* ++
STAPHYLINIDS	*12*	*89*	*118* ++	*72*	*368* ++	*284* ++	*799* ++
COLEOPTERA LARVAE	*11*	*19* ++	*21* +	*21* +	*69* ++	*78*	*143* ++
TOTAL INVERTS (inc. others unlisted)	*376* +	*1576* ++	*1773* ++	*2514* ++	*12629* ++	*7648* ++	*5673* ++

\+ *significant (P<0.05)*
\++ *highly significant (P<0.01)*

The results reveal that all the invertebrate groups looked at were significantly hetrogeneous in their distribution amongst sites, and by implication, other groups not studied probably were also. It is important to note, however, that the change in order of significance within a group is a reflection of an increase in size of data set, and not necessarily a greater uneveness in distribution amongst sites.

Non-significant differences for the distribution of a number of invertebrate groups between sites at certain periods during sampling, obliges, at times, an acceptance of the null hypothesis i.e. that there was no difference in totals between sites. This, however, is the result of a small data set rather than a lack in biological trend. A total of 159 Araneae collected on 15 April, were not significant ($P>0.05$) in their habitat distribution, but highly significant ($F=_{(1,112)}38.82$;$P<0.01$) in the following collection when 831 were counted. In other groups such as Diptera larvae, however, unequal distribution was marked even when the numbers collected in traps were relatively low. Though all groups examined showed heterogeneous distributions, the order of significance for these varied according to how many members were counted belonging to that group and the specificity of habitat requirement, or diversity in spatial niches of its constituent species. Diptera larvae, for example, have a narrower potential range of habitats that they can occupy compared to Araneae.

These results highlight the fact that within a relatively small area of moorland habitat, there are actually an array of habitat types that give rise to differential success amongst neighbouring invertebrate populations. To look at how sites vary in relation to what species within a group are present, close study was made of members of the family Tipulidae (within the group Diptera).

3.2 Tipulid distribution

Fig. 2. demonstrates any pattern of tipulid distribution that may be occurring at the individual site level by comparing data for 1994 spring tipulid totals with totals for the same period in previous years.

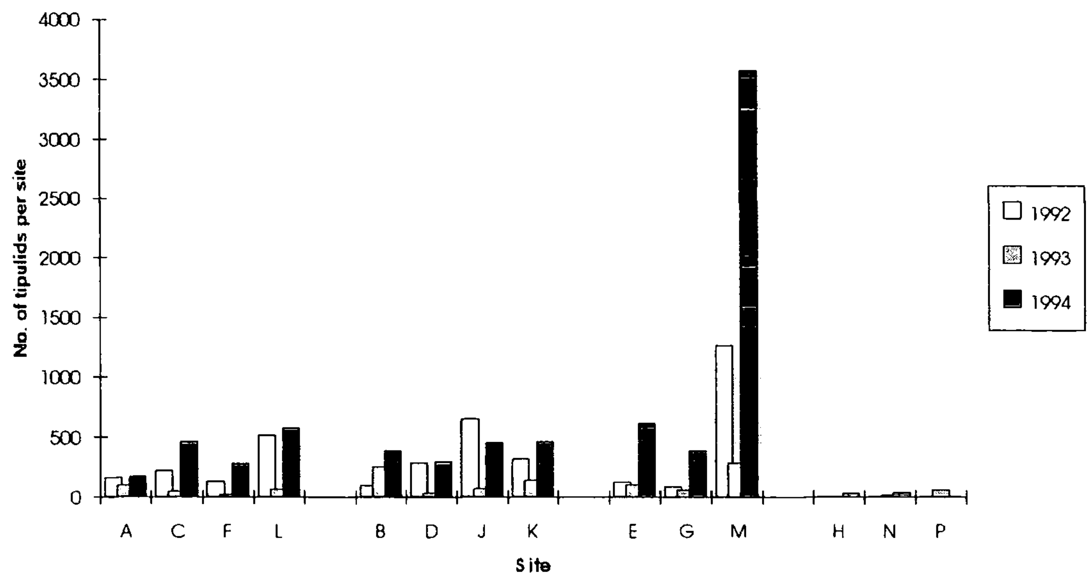


Fig. 2. Distribution of total tipulids captured in 10 pitfall traps at each site on Chapel Fell, between early May and early July, 1992 - 1994.

In total, the dry peat sites yielded the most tipulids during 1994, producing 4612 tipulids - approximately 1.5 times the number found at the other site groupings added together. This, however, was largely due to the overall abundance of tipulids at site M (n = 3575), and not a general characteristic of dry peat sites, because at G, much lower numbers were present (n = 388). This wide variation in numbers between dry peat sites is expressed by the coefficient of variance value (C of V = 1.16), which is much higher than those for mineral (C of V = 0.48); wet peat (C of V = 0.18), and hag sites (C of V = 0.71).

From these data it appears that a reliable judgement relating to tipulid distribution generally, cannot be made upon the basis of these site categories. Neither is it appropriate, as the mineral soil habitat typically has different species than those found on peat soil (Coulson, 1959). Furthermore, an attempt to find a simple correlation between soil mositure content and numbers of tipulids at individual sites is only appropriate within soil categories, as different soil types have different water holding capacities depending on their structure and organic matter content (Crump,1913).

As with other invertebrates, tipulids displayed an unequal distribution amongst study sites that was significant (Table 1); and Fig. 2 displays this distribution together with the distribution of tipulids in previous years. One site in particular (M), as already mentioned, was extremely favourable for tipulids especially *Tipula subnodicornis* and *Trichyphona immaculata* (Figs. 3 & 4); whilst at other sites (L and E), tipulids were only moderately successful; other sites (H and A), featured very few individuals. The degree of relative success by tipulids overall, appeared to be a more constant feature at some sites e.g. M, than others e.g B, although in the lean year of 1993, differences between site totals became much less. Actual numbers were particularly constant at mineral site A and hag sites H, N and P, which consistently featured low numbers of tipulids (or any invertebrates). These sites would seem to have less potential for tipulid success than other sites, and thus the difference between good and bad years is only small.

The pattern of distribution for tipulids overall in Fig. 2 reflects mainly that of the dominant species *Tipula subnodicornis* and the second most common species *Trichyphona immaculata*. The distributional pattern of *Limnophila meigeni* was slightly different but was masked by their dominance in numbers. Most species could be found on a range of sites (bar the hag sites H, N and P) possibly due to overspill from favoured areas. *Molophilus ater*, however, was found almost exclusively at site M - as it was in 1992 (Appendix I).

The two species that contributed most to tipulid abundance during 1994 were *Tipula subnodicornis* and *Trichyphona immaculata*. The distribution of these species along with others, are shown in Appendix I. Fig. 3 below, presents these data graphically for *Tipula subnodicornis*, comparing its distribution with previous years and Fig. 4 does the same with *Trichyphona immaculata*.

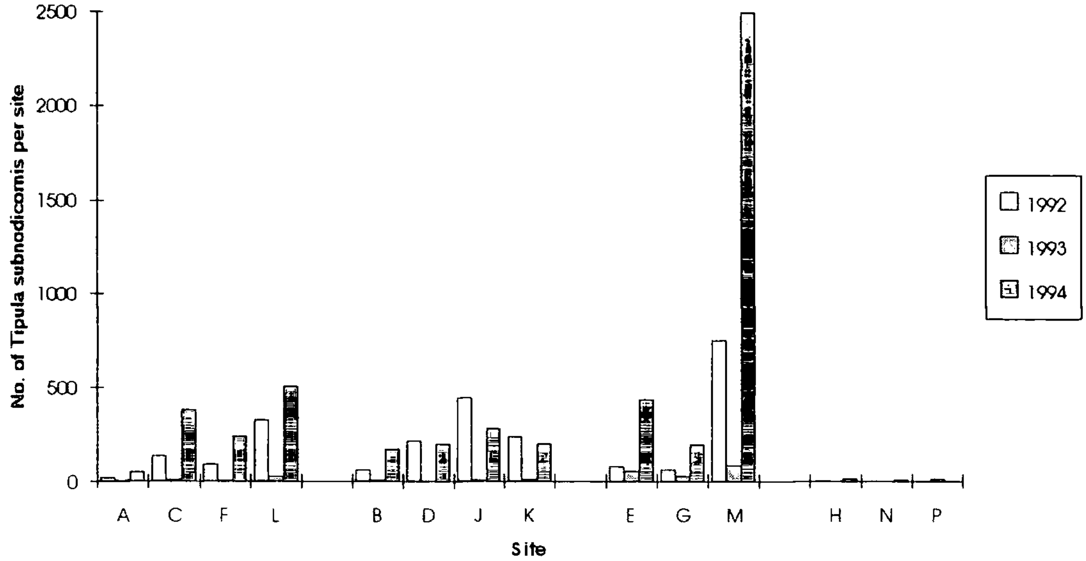


Fig. 3. Distribution of *Tipula subnodicornis* captured in 10 pitfall traps at each site on Chapel Fell, between early May and early July, 1992 - 1994.

Changes in abundance of *Tipula subnodicornis* within different habitats, have been calculated by comparing its numbers at each site on Chapel Fell in 1993, with numbers captured in 1994 (Table 2). The change in abundance at each site is expressed as the ratio of numbers in 1994 to the numbers in 1993, i.e. the 1994 total divided by the 1993 total for each site.

Table 2. The change in abundance of *Tipula subnodicornis* captured in 10 pitfall traps at each site on Chapel Fell, between May and July, 1993 - 1994. The amount of change at each site is expressed as a ratio of 1994 totals to 1993 totals.

Site	A	B	C	D	E	F	G	H	J	K	L	M	N	P
1993	7	5	9	2	55	8	28	2	6	9	28	83	4	14
1994	52	172	382	198	436	239	197	12	279	200	506	2496	10	3
Change	+45	+167	+373	+196	+381	+231	+169	+10	+273	+191	+478	+2413	+6	-11
'94:'93	7.4	34.4	42.4	99.0	7.9	29.9	7.0	6.0	46.5	22.2	18.1	30.0	2.5	0.2

Although, in 1994, site M was responsible for just under half of the total increase (49%) of *Tipula subnodicornis* abundance on 1993 figures at Chapel Fell, this site did not have the highest ratio of increase of the species between these years. Instead, the greatest ratio of increase was at site D, a site which had only a small share (3.8%) of the total number of *Tipula subnodicornis* captured.

Site M, however, evidently provided favourable conditions for *Tipula subnodicornis* development, as in 1993 and 1994 this site featured most individuals (Fig. 4, Appendix I). Comparing totals from these two peat sites , it would seem that both had provided adequate conditons for successful larval development between June/July 1993 to June/July 1994, but at site D a constraint prevented abundance reaching as high as at other peat sites or, indeed, even as high as totals at the same site in 1993 when overall *Tipula subnodicornis* numbers at Chapel Fell were less. The reason for this is probably due to soil conditions during early larval development in 1992 at site D, which caused a low number of adults to emerge in the spring of 1993, and thus the potential of *Tipula subnodicornis* to populate the habitat with higher numbers was limited.

Taking the totals of *Tipula subnodicornis* at sites D and M in 1993, a rough calculation can be made on the potential number of offspring they may have been able to produce, based on the sex ratio of 3 : 2 adult males to females found in *Tipula subnodicornis,* and the average number of eggs contained by the female (Coulson, 1962), and assuming all females become fertilised (Table 3). These are indeed gross assumptions as not all these eggs will necessarily be laid, but this method allows some degree of comparison of the potential number of offspring with the actual number sampled at those sites in 1994.

Table 3. The potential number of eggs laid in June at sites D and M based on:- a 3 : 2 ratio of adult males to females, and an average number of 240 eggs contained by a fertilised female *Tipula subnodicornis*.

	Site D	Site M
Number of adults in 1993:	2	83
Number of females in 1993:	0.8	33.2
Potential number of eggs:	192	7968

Comparison of the potential number of offspring in Table 3, with the actual number sampled at these sites in 1994 (Table 2), shows that much higher mortality occured at site M (67%), than at site D (-3%). Site D having minus mortality, suggests that this site was either under-represented by pitfall traps in 1993, or that overspill from other areas occurred. Moreover, what these figures suggest is that at site M, and also E for example, density-dependence limited increase, whilst at sites D and J, the density-dependence mechanism allowed an increase. From these results, we may conclude that density dependence appears to have controlled numbers in favourable peat habitats where numbers were relatively high in 1993, but has allowed an increase in the peat areas where, in 1993, numbers were relatively low. As previously mentioned, density-dependence is not the only control on numbers, and at site H for example, the over-riding factor for abundance limitation would be likely to do with the periodical dessication which the habitat has the potential for. The increase of *Tipula subnodicornis* on mineral sites is neither an effect of density-dependence (at least directly), but more probably the result of overspill from other peat areas.

1993 tipulid abundance would have been related to soil conditions during early lifecycle stages after eggs were laid in June, 1992. Apart from dry conditions at hag site H corresponding with very few tipulids present, soil moisture data taken in July of 1992 (Appendix II) does not show a correlation with *Tipula subnodicornis* numbers, but does show how variable soil moisture, particularly amongst peat sites, can be during dry weather. During these dry periods, differences in soil moisture content from site to site may be greater according to the varying capacity for water retention amongst different soils.

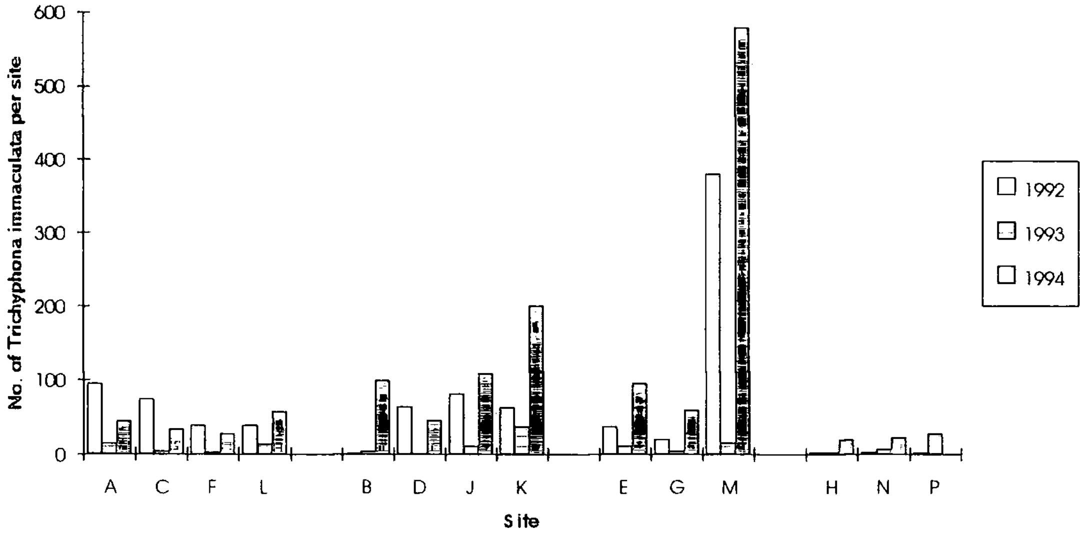


Fig. 4. Distribution of *Trichyphona immaculata* captured in 10 pitfall traps at each site on Chapel Fell, between early May-April and early July, 1992 - 1994.

Trichyphona immaculata followed a similar pattern to *Tipula subnodicornis* on the dry peat sites from 1992 through to 1994, but within other categories it differed. In contrast to *Tipula subnodicornis*, it did not exceed 1992 totals on most mineral soils but did at each site in the dry peat areas. Furthermore, at hag site P, it disappeared completely, yet in 1993 was present in numbers comparable to other wet and dry peat sites.

3.3 Tipulid abundance

Tipulids were first collected in pitfall traps lifted on 27 May, and during the following four weeks their high abundance made them an appropriate group to study for habitat distribution.

Numbers of emerging tipulids during the spring of 1994 reached very high levels, in comparison to spring of the previous two years, particularly in comparison to 1993 totals. Table 4. demonstrates this large increase in tipulid abundance.

Table 4. Totals for the main tipulids on Chapel Fell and their percentage proportions of spring emergence figures, 1992 - 1994

Species	1992	% of total	1993	% of total	1994	% of total
Tipula subnodicornis	2426	62.5	260	28.6	5182	69.1
Trichyphona immaculata	900	23.2	160	17.6	1396	18.6
Limnophila meigeni	227	5.8	427	47.0	514	6.9
Molophilus ater	85	2.2	10	1.1	370	5.0
Tipula varipennis	245	6.3	53	5.8	35	0.5
Total	3883		910		7497	

A number of tipulid species contributed to the overall tipulid totals for spring 1994, but some were more notable than others in their abundance. It can be seen from the table that the largest proportion (69.1%) of emerging tipulids were *Tipula subnodicornis*, and these subsequently dominate the pattern in total tipulid emergence. The next most common species were *Trichyphona immaculata* followed by *Limnophila meigeni*; but these two species together made up only about 25% of the total tipulid numbers for 1994.

The percentage proportion values for *Tipula subnodicornis*, *Trichyphona immaculata* and *Limnophila meigeni*, each resembled percentage proportion figures for the spring emergence of 1992. In 1993, however, *Tipula subnodicornis* and *Trichyphona immaculata* experienced a population crash, that reduced their total populations markedly. The chi-square value for differences between years 1992 - 1994, of *Tipula subnodicornis* totals, for example, is highly significant ($\chi^2_{(26)}$=1214;P<0.01). Whatever may have devastated populations of the other species in 1993, did not suppress numbers of *Limnophila meigeni*, but allowed an eight times increase in its percentage proportion to 47% of spring emergence totals and a virtual doubling of its numbers.

Tipula subnodicornis and *Trichyphona immaculata* appear to be subject to environmental conditions that do not have the same effect on *Limnophila meigeni*. A mechanism of density dependence as suggested earlier, however, ensures that they return to high abundance when favourable conditions arrive.

All tipulid species, except *Tipula varipennis*, showed abundance levels higher in 1994 than in 1992 and 1993. These abundance figures suggest that preceeding conditions, during the period of egg laying and first larval instars in the spring of 1993, were especially favourable for the survival of tipulids generally on Chapel Fell, compared to the other years. This resulted in the subsequent high emergence of tipulids, particularly *Tipula* *subnodicornis*, during early June, 1994. There is though, a slightly erratic nature to population change in tipulids and subsequently the trend for total tipulid numbers from 1992 to 1994 (intermediate - low - high), is not matched by *Limnophila meigeni,* which consistently increased, and *Tipula varipennis,* which consistently decreased, even in relation to its percentage proportion of totals.

3.4 Tipulid spring emergence

The characteristic emergence/disappearance of this family of Diptera is depicted in Fig. 5. Data from spring 1992 and 1993, also presented in this figure, reveals emergence to have begun earlier in previous years, than in 1994. Peak abundance for 1993, however, coincides with that for 1994, but with a much smaller abundance (Table 4) and with only a gradual curve to the graph, compared to the more dramatic rise and fall of Chapel Fell's tipulid emergence in 1992 and 1994. Peak abundance in 1994 arrived abruptly and followed the same pattern as 1992 but with almost twice the abundance for 1992 (Table 4), and was recorded two weeks later.

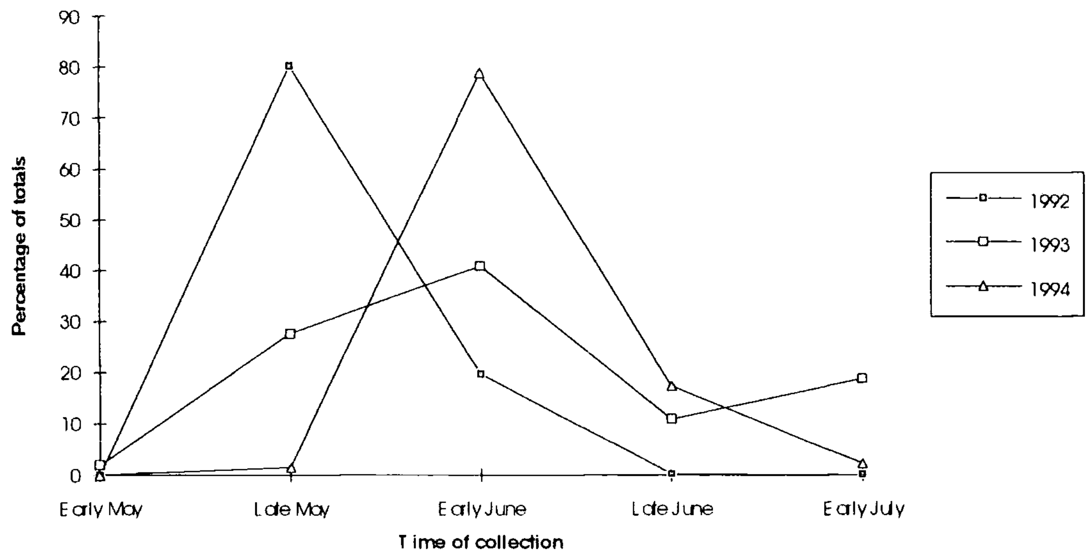


Fig. 5. Spring emergence of tipulids, captured in 10 pitfall traps at each site on Chapel Fell, as a percentage of their total abundance, between early May and early July, 1992 - 1994.

For the three most abundant spring emerging species on Chapel Fell in 1994 - *Tipula subnodicornis*, *Trichyphona immaculata* and *Limnophila meigeni* - peak abundance arrived two weeks later than in previous years (Figs. 6-8); in early June rather than May for *Tipula subnodicornis* and *Trichypnona immaculata*, and late June instead of early June for *Limnophila meigeni*.

It is the high numbers of *Tipula subnodicornis* and *Trichyphona immaculata* particularly, (Table. 4), which give shape to the 1994 curve in Fig. 5, previously described.

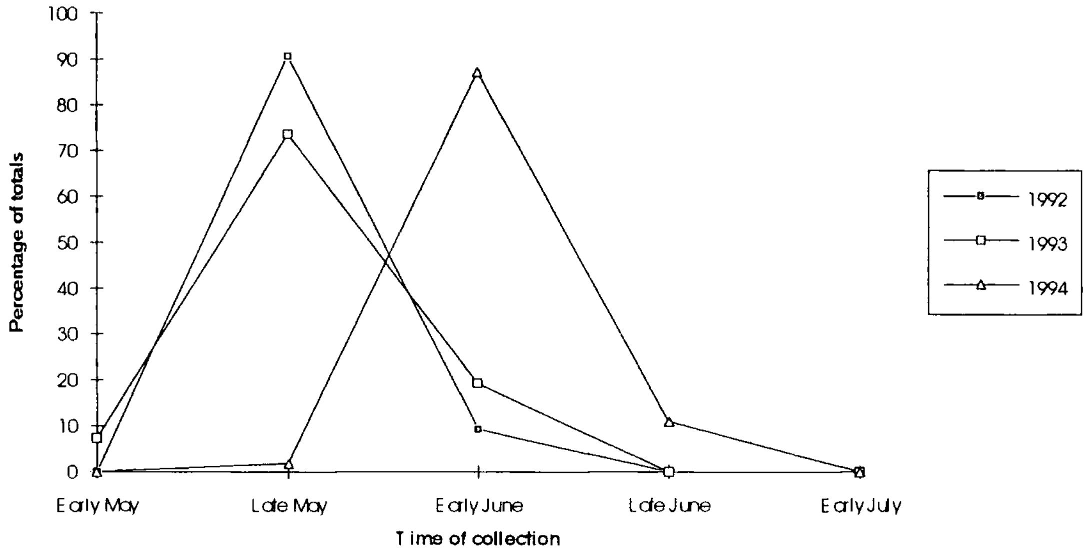


Fig. 6. Spring emergence of *Tipula subnodicornis*, captured in 10 pitfall traps at each site on Chapel Fell, as a percentage of their total abundance, between early May and early July, 1992 - 1994.

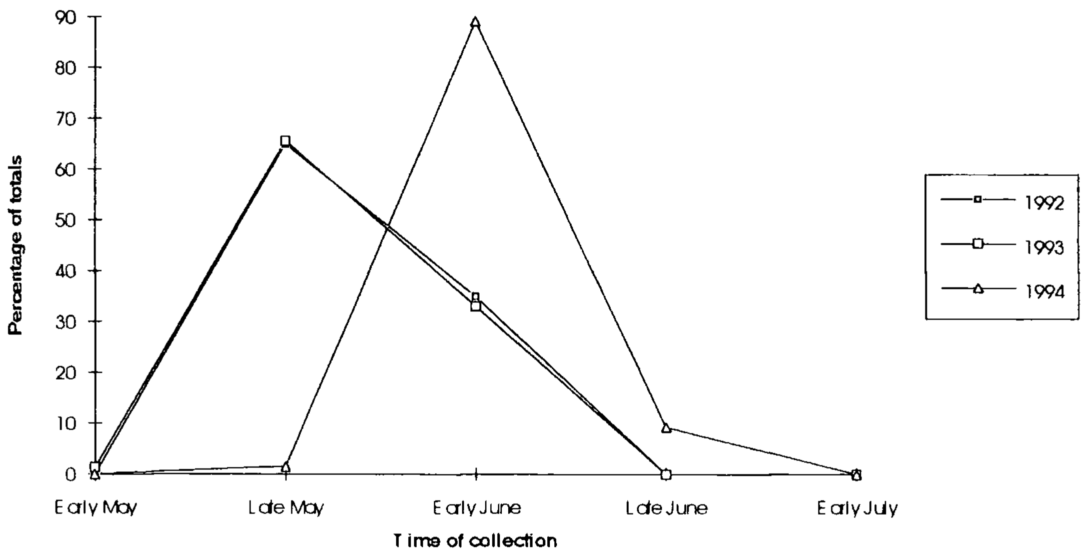


Fig. 7. Spring emergence of *Trichyphona immaculata*, captured in 10 pitfall traps at each site on Chapel Fell, as a percentage of their total abundance, between early May and early July, 1992 - 1994.

Though *Limnophila meigeni* emerged two weeks after the other species (Fig. 8), it did not have much impact on emergence totals (Fig. 5) as it was less common.

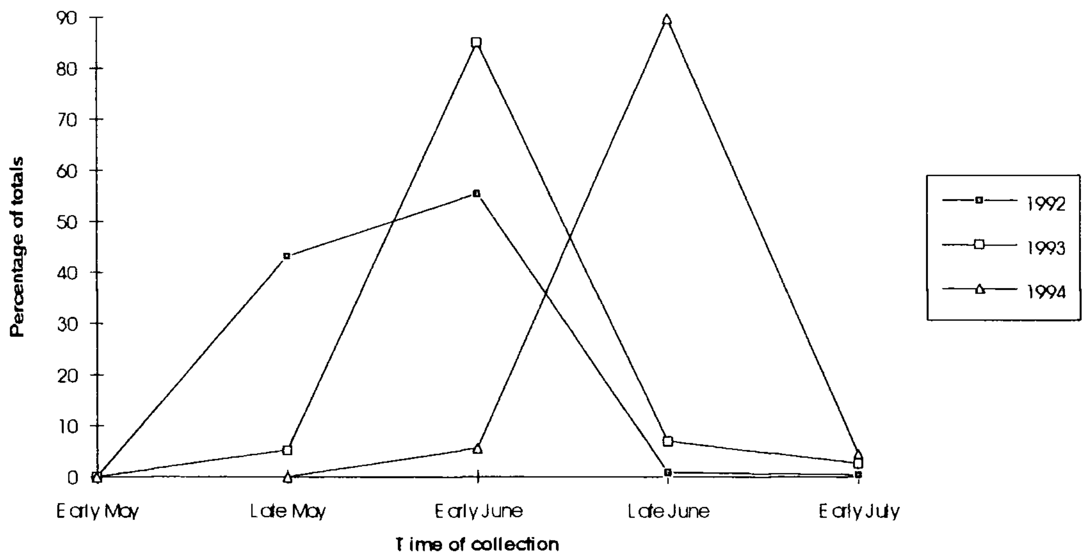


Fig. 8. Spring emergence of *Limnophila meigeni*, captured in 10 pitfall traps at each site on Chapel Fell, as a percentage of their total abundance, between early May and early July, 1992 - 1994.

Unlike other species, *Molophilus ater*, which made up only 5% of tipulid totals in Spring, had an abrupt emergence to peak levels and a peak abundance which coincided with the two previous years' timing in early June (Fig.9). Furthermore, its pattern of emergence was opposite to previous years, with a more gradual decline after peak abundance.

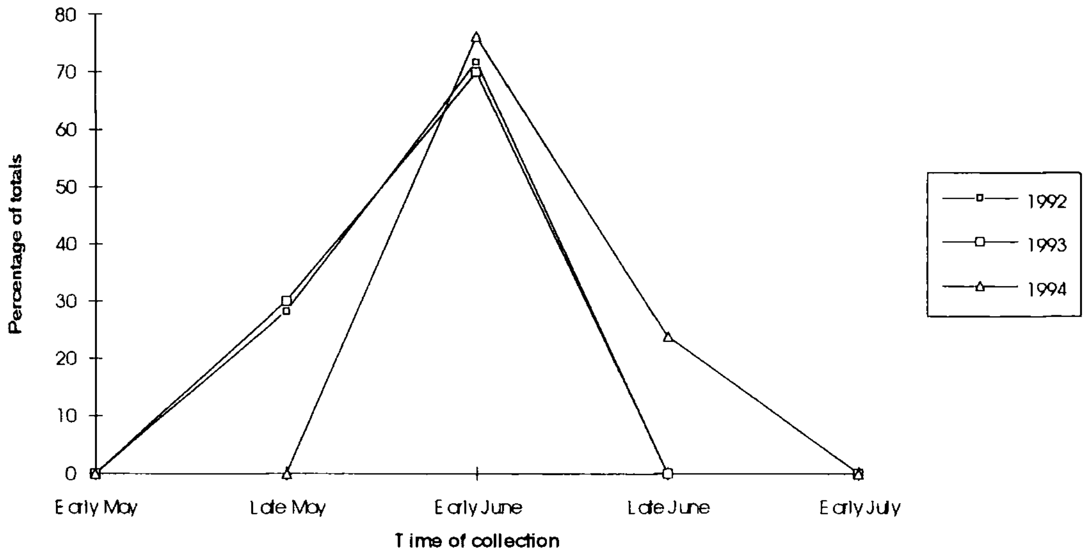


Fig. 9. Spring emergence of *Molophilus ater*, captured in 10 pitfall traps at each site on Chapel Fell, as a percentage their total abundance, between early May and early July, 1992 - 1994.

3.5 Differences relating to use of new and old pots in sampling

During sorting of the pitfall catches, it was noticed that a higher number of invertebrates occurred in the new traps, than in the old (Appendix III). This difference of numbers in new and old traps, however, decreased as time went on and so, with each fortnightly collection, the ratio of invertebrates between trap types became less, as displayed in Fig. 10.

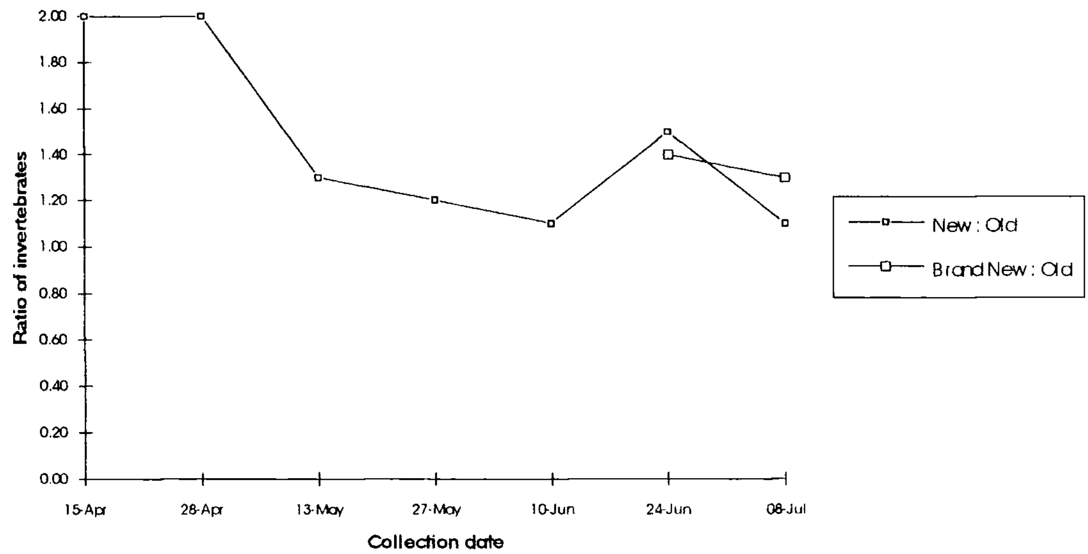


Fig. 10. Ratio of invertebrates in New : Old traps used for sampling on Chapel Fell from 1 April to 8 July, 1994. Brand new traps were reintroduced into the monitoring on 10 June.

Table 5. gives the ratios of differences in numbers of organisms collected in new and old traps from April to July 1994 (Appendix III). Two-way ANOVA, with new and old trap replicates at each site, were executed on the data to test the null hypothesis that no differences in numbers occurred between trap types. Ratios are given - new : old, or brand new : nearly new : old, where old = 1. The significance of these ratios are indicated to one decimal place. The terms given:- brand new, nearly new, e.t.c., are to distinguish between the lenghth of time traps had been in use in the field. At the start of monitoring in April, all new traps were essentially brand new, however, to distinguish these from traps introduced into the monitoring on 10 June, they are referred to as 'new', while the traps introduced later are 'brand new'. Further differentiation is made by referring to the new traps collected on 24 June and 8 July which had been in use since 1 April, as 'nearly new'.

Table 5. The relative effectiveness of New and Old pitfall traps, on Chapel Fell between April and July, 1994. Numbers caught in each trap type expressed in ratios; New : Old, till 10 June, and Brand New : Old thereafter, with significance of an unequal ratio indicated. On 24 June and 8 July, this refers only to the ratio between Brand New and Nearly New.

Trap collection date	15 Apr	28 Apr	13 May	27 May	10 Jun		24 Jun	8 Jul
TIPULIDS	*absent*	*absent*	*absent*	*0.4*	*0.9*	BN	*1.0*	*1.3*
				++	++	NN	*1.2*	*1.2*
OTHER DIPTERA	*3.4*	*1.9*	*1.3*	*1.3*	*1.2*	BN	*1.3*	*1.4* +
		+		++		NN	*1.5*	*1.0*
DIPTERA LARVAE	*1.5*	2.8	2.5	2.1	*1.7*	BN	*4.5*	*1.0*
						NN	*3.8*	*1.1*
ARANEAE	*3.0*	2.2	*1.6*	*1.5*	*1.6*	BN	*1.6*	*1.5* +
	++	++	+	++	++	NN	*1.7*	*1.1*
CARABIDS	2.0	*1.2*	*1.3*	*1.2*	*1.6*	BN	*1.1*	*1.1*
			++		++	NN	*1.5*	*1.0*
STAPHYLINIDS	2.3	*1.0*	*1.3*	*1.3*	*1.4*	BN	*1.6*	2.1
					+	NN	*1.2*	2.0
COLEOPTERA LARVAE	*1.0*	2.0	*1.5*	*1.9*	*1.1*	BN	*1.7*	*1.3*
						NN	*1.4*	*1.2*
TOTAL INVERTS	2.0	2.0	*1.3*	*1.2*	*1.1*	BN	*1.4*	*1.3*
	++	++	+	+		NN	*1.5*	*1.1*

+ significant ($P<0.05$) BN = brand new
++ highly significant ($P<0.01$) NN = nearly new

Total invertebrates were occurring in new traps at significant levels up until 27 May ($F=_{(1,12)}4.98; P<0.05$), but on 10 June, the marginally higher number of invertebrates in new traps was not statistically significant. Thereafter, comparing new traps generally, with old traps, showed the higher numbers occurring in new traps to be highly significant; ($F=_{(1,12)}22.71; P<0.01$) on 24 June, and ($F=_{(1,12)}7.84; P<0.01$) on 8 July.

To investigate further if trap selection was occurring in all or just some groups, comparison was made of numbers for the most commonly found invertebates in new and old traps. The groups looked at were the following: other Diptera, Diptera larvae, carabids, staphylinids, Coleoptera larvae and Araneae.

Except on two occasions where numbers were similar and low in each trap type - Coleoptera larvae (April 15), and staphylinids (Apr 28) (Appendix III); the ratio of these invertebrates in new to old traps was always greater than one (Table 5). On no occasion amongst these groups were there fewer members occurring in new traps.

As with numbers for total invertebrates, the predominant pattern in ratios for individual groups over time was a levelling out of the differences between the two trap types (new/old). This trend suggested that either an environmental factor i.e. to do with the change in season, was interacting with the influence of trap type, or, that whatever innate factor new traps possessed as an advantage over old in capturing invertebrates, was decreasing with time. A brand new set of traps were therefore introduced on 10 June, to see if:-

a) they would produce any difference in results to the now 'nearly new' traps, (traps that had been in use from new since April 15 1994); and
b) they would produce an increased difference once more from the old traps (traps that had been in use for a number of years), comparable to that on 15 April.

On the first occasion of introducing these traps (10 June), two brand new traps replaced two nearly new traps in each site transect, but in the following fortnight (June 24), another was included so that three brand new traps were laid out - amongst three nearly new and four old. On every other occasion previously, five old traps had been used.

Results collected on June 24, comparing two brand new traps with two nearly new traps, and with two old traps, again showed a higher numbers of invertebrates, within each taxa looked at, in new traps compared to old with an F value that was highly significant ($F=_{(1,12)}22.71; P<0.01$) (Appendix III). There did not, however, seem to be a predictable difference between numbers in brand new or nearly new traps for this sampling date, and thus, overall, the ratio between brand new and nearly new traps was almost equal. When three traps of each type were used, in the final fortnight of sampling (ending 8 July), higher numbers of invertebrates overall were found in brand new pots and lowest in old, as exemplified by the ratio 1.3 (brand new) : 1.1 (nearly new) : 1 (old), for total invertebrates, but ANOVA on these overall results revealed them to be outside levels of significance.

The one exception to the trend of higher numbers in brand new traps on 8 July, amongst individual groups were Diptera larvae, which were never common in pitfall traps, and the low total counts of these from each trap type gave only a difference of three individuals between highest and lowest catches . Otherwise, numbers were either the same between trap type e.g staphylinids, or higher in the brand new traps e.g Araneae, and other Diptera (Appendix III). The latter two also gave values of significance to this unequal distribution between trap types:- ($F=_{(1,104)}6.96; P<0.05$) for Araneae; and ($F=_{(1,104)}4.86; P<0.05$) for other Diptera.

As there was a lack of a significant difference between overall numbers in brand new traps and nearly new traps, collected on 24 June and 8 July, it follows that the decrease in capture efficiency of new traps, from 28 April onwards, was not due to the decay of an innate factor, but rather the result of an environmental influence bearing effect.

If the higher efficiency of new traps over old, was merely due to an innate factor related to their age (in weeks), then it would be expected that re-introducing brand new traps into the monitoring on 10 June, would have resulted in a two times higher number of invertebrates within them, than in the old traps when they were collected on 24 June. This was not the case, as the capture efficiency of brand new traps on this date was only 1.4 times that of the old, and on 8 July, 1.3 times.

Comparison made using chi-square, of numbers found in brand new traps on 24 June with expected values based on the 2 : 1 ratio that occurred in (brand) new : old traps collected on 15 April, showed differences to be highly significant ($\chi^2_{(12)} = 129; P<0.01$). This establishes that the ratios between new traps collected on 24 June, were significantly less than between new and old traps introduced on 1 April.

Ratios did seem to increase to some extent after the introduction of brand new pots on 10 June, but this occurred also in the nearly new traps and so the cause was something other than trap age. Furthermore, a comparison using a paired t-test, between numbers in nearly new traps on 10 June and on 24 June showed that these differences in numbers were not significant($T_{(12)} = 1.4$), and thus were not a significant disruption to the trend of decreasing ratios.

Statistical analysis using ANOVA was applied to the data to establish:- whether to accept the null hypothesis that no difference in numbers occurred between new and old traps; or alternatively, if trap type led to a significant difference in numbers of invertebrates. Groups such as Coleoptera larvae and Diptera larvae, while demonstrating a tendency to select new traps, did not reveal significance, probably as a result of their relatively low numbers. Araneae, on the other hand - ubiquitous in distribution and throughout the weeks of sampling, were usually highly significant in their selection of new traps e.g ($F=_{(1,104)}32.40; P<0.01$) on 28 April. Between these extremes; other Diptera, carabids and staphylinids were on occasions significant or highly significant in selecting new traps, depending on numbers (Appendix III). Even when not at significant levels, however, this tendency of higher numbers in new traps was always apparent.

For each fortnight of sampling, higher numbers of invertebrates occurred in new traps overall, with this unequal distribution being, on each occasion, either significant or highly significant. To start with, in the first two collections when the ratio was 2:1, selection for new traps was highly significant; ($F=_{(1,104)}8.78;P<0.01$) on 15 April, and ($F=_{(1,104)}30.45;P<0.01$) on 28 April. Despite higher numbers of invertebrates in subsequent weeks than in the first week, the ratio became less with a corresponding decrease in significance ($F=_{(1,104)}4.98;P<0.05$). Moreover, on 10 June, when a large (x4.8) increase on previous fortnight totals was collected, results were not significant. The large increase in total invertebrates was mostly due to the abundance of Diptera, notably *Tipula subnodicornis*.

Following their emergence, it was possible to investigate tipulid distribution amongst traps. In contrast to all the other categories observed, including other Diptera, tipulids appeared to be selecting in favour of old traps on 27 May and 10 June, as they emerged to peak abundance; and an on both occasions, this selection was highly significant; ($F=_{(1,104)};8.06;P<0.01$) and ($F=_{(1,104)}7.09;P<0.01$) respectively. It is the high numbers of tipulids upon 10 June, marginally favouring old traps at a ratio of 1.1 (old) : 1 (new), that also decreasesd the ratio for total invertebrates occurring between old and new trap types on this date, causing it to lose significance despite results of significance in staphylinids and high significance in carabids and Araneae.

Analyses of variance applied to the results for the final two collections showed, on 24 June, that any observed differences in numbers between brand new traps and nearly new traps, were not statistically significant. On 8 July, however, when three traps of each type were used per transect, an unequal distribution between brand new and nearly new traps was significant in other Diptera ($F=_{(1,12)}4.86;P<0.05$), and Araneae ($F=_{(1,12)}6.96;P<0.05$); these invertebrates were occurring in higher numbers in brand new traps. Overall, however, differences between numbers in brand new traps and nearly new traps were not significant although slightly higher numbers did occur in brand new traps (Appendix III).

4.0 DISCUSSION

4.1 Invertebrate distribution

The distribution of tipulids was looked at separately from the rest of the invertebrates found on Chapel Fell, due to their overwhelming dominance in numbers compared to other families and groups. Inclusion of them in an overall analysis of invertebrates would have obscured any other pattern that other invertebrate groups may have presented.

Comparing Fig. 1 (distribution of invertebrates), with 1994 data on Fig. 2 (distribution of tipulids), shows that while certain similarities occurred, such as low pitfall totals at site H, the extremely high abundance of tipulids at M was not matched to the same extent by other invertebrates groups even when added together. Difference also lies in the fact that mineral soils showed more variation between sites for tipulid totals (C of V = 0.48), than for other invertebrates overall (C of V = 0.12), whereas amongst the wet peat sites, coefficient of variance from the mean total was greater in other invertebrates (C of V = 0.34), than in tipulids (C of V = 0.18).

Though no significant differences in mean values occurred between totals from the three site categories given for the area by Coulson & Goodyear (1989), variation in the degree of heterogeneity for invertebrate totals from site to site was evident between the categories as shown in Fig. 1, and by the values for coefficient of variance.

The explanation for this is not given simply by organic matter, or soil moisture content recorded on 22 July, for these alone bore no correlation to numbers of invertebrates. Instead, other factors would seem to be important. Site F for instance, had similar vegetation to the other mineral sites, but also differed from them in that it was close to an area of blanket bog - which if similar to a location such as site D, may have had a lowering influence on the local population of mobile invertebrates such as carabid beetles, which, in woodland areas at least, prefer a grass habitat than a habitat predominated by a litter substrate (Greenslade, 1965).

At the peat sites, invertebrate totals were found to be very variable from site to site. Here were found the most extreme results - highest and lowest (H and M). The solution to these differences may be found in site structure. While both had peat soil and a similar soil moisture (on 22 July) and organic matter content, site H had sparse vegetation cover with soil erosion forming hags, while M was a level vegetated site with *Juncus squarrosus* alone giving 48% cover. Accordingly, site H, is more vulnerable to dessication during dry periods, with evaporation occurring from the steep exposed hag faces, as was indicated in July 1992, when site H had 9% less moisture than all other peat sites

The exposed hag faces may themselves, be unsuitable for many invertebrate groups that rely on vegetation as cover and a food resource. Individuals of some carabid species can cover relatively large distances e.g *Pterostichus madidus,* which can travel 10m per day, may be less represented in pitfall traps (Greenslade, 1964). Mineral sites C and F, however, are linear habitats occuring alongside a stream, but these did not have much lower totals than other sites and therefore periodical dessication of the habitat is the most likely cause of low numbers of invertebrates within the hag areas.

Other 'dry peat' sites, E and G, displayed pitfall totals similar to M. These sites all had in common a fairly high cover of *Eriophorum vaginatum*, providing vegetational cover and a food source for soil fauna.

Wet peat displayed the most variable invertebrate densities beteen sites i.e. the highest coefficient of variance between each site in terms of invertebrate totals. The lowest number of invertebrates amongst these sites were at site D (shallow peat) which featured an organic content that was 10% less than the other peat sites, while the highest invertebrate totals were at site J. In July 1994, the water content of these two sites were very similar; 84% (D), and 85% (J), but organic content of soil, as well as soil depth, is a factor that can affect water holding capacity and in July 1990, differences between these sites were much greater; 43% (D) and 64% (J).

Site J also featured more structural/vegetational diversity than others. Vegetational structure can affect microclimatic conditions and has been shown to influence vertical distribution of insects such as Homoptera which migrate to different heights within the vegetation during the day (Coulson and Whittaker, 1978). Accordingly, this may also translate to lateral distribution for, if the opportunity for such a migratory mechanism is not present in some animals, it may induce them to seek another habitat. Habitat selection relating to an environmental factor such as microclimate or substrate is suggested by Thiele (1977) for carabid beetles.

Intermediate to these sites in terms of invertebrate totals were B and K, similar sites of high vegetation cover (*Eriophorum vaginatum* and *Deschampsia flexuosa*).

Results from analyses of variance showed that all animal groups looked at, displayed a varied distribution between sites that was significant. For some, such as Diptera larvae, this distribution was significant even when numbers of them were low (26) on 27 May, while others, such as Araneae, were not significant even with much higher numbers (159) counted on 15 April. The significance given to the abundance distribution of groups of organisms by ANOVA, is a reflection of the reproductive success and survival rate of certain organisms within particular habitats, and subsequently partly an indication of the diversity of spatial niches within the categories of organisms being studied. Niche separation for various species of Diptera larvae for instance, is likely to be narrow due to their requirement of a soil habitat with a high moisture content, whereas niches that can support Araneae are wide ranging (Savory, 1964). Furthermore, the ANOVA results may reflect the dispersal capabilities of organisms, e.g. Diptera larvae have limited mobility, while Araneae can move considerable distances along the ground (Jones-Walters, 1989), and thus may stray outside their normal species habitat.

The distribution of some species' abundance within adjacent habitats has also been suggested by Walker (1985), to be evidence of habitat choice. In this study, proximate sampling sites such as C and D (Map 1) - while differing markedly in their invertebrate catches, are divided by a stream and therefore cannot be considered in this way, for non-flying invertebrates.

This study failed to find correlation with invertebrate numbers in soil moisture content at different sites in July 1994 as all peat sites were relatively wet. What the results do reflect, however, is the relative stability of the mineral soil habitat for invertebrates compared to peat soils. While soil moisture levels in mineral soils are generally much lower, capillarity of the soil can provide water from lower levels during dry periods of weather. Peat soils, do not have this characteristic and during drought, water retention will vary considerably, according to habitat structure, depth of soil and amount of organic content. Sites such as D (shallow peat) and H (hag peat) therefore, although having soil moisture levels comparable to other wet sites in July, had lower numbers of invertebrates which were probably due to periods of dry weather when, in comparison to other sites, they retained less moisture. During these periods, a high degree of mortality would have occurred especially in small, young invertebrates.

4.2 Tipulid distribution

In comparison to their larval stages, adult male tipulids are generally fairly mobile. Accordingly, adult individuals of these Diptera were found at all of the study sites on Chapel Fell, with one species in particular - *Tipula subnodicornis* - being collected from every site. The abundance of this species evidently may have caused an overspill of individuals into areas where normally it would not be expected to be present, i.e. the mineral sites (A,C,F,L) as its larvae are restricted to peat (Coulson, 1962).

The results demonstrate in Table 2, that the 12 months from May/June 1993 to May/June 1994 were particularly favourable for tipulids in general, allowing a two times increase on 1992 totals and a sixtimes increase on 1993 totals. This pattern of increase was similar at many of the study sites, with an obvious example being site M, which has proved to be the most favoured site for tipulids in previous years.

Though magnitudes vary, this pattern of change was also present at other dry peat sites (E and G). The pattern within the dry peat locations therefore, has been a consistent one of increase, above totals for 1992 and 1993, matching the overall pattern for tipulids on Chapel Fell (shown in Table. 4). Hag sites (H,N,P), however, continued to feature very few tipulids, as in previous years.

In wet peat areas there was not concordance with the general pattern. Although, in every case, numbers overall were up on 1993 totals, at site D there was little difference between 1992 and 1994 totals, and at site J, numbers actually decreased (Fig. 2). It appears that at these sites a restraint occurred on abundance increase, which is demonstrated for the most common species, *Tipula subnodicornis.* Evidently, conditions for developing larvae from July onwards in 1992, were poor enough to depress their numbers to such an extent that in the following spring, populating of these sites was left to only a few egg-laying adults (Table 3). Subsequently, though, these two sites, had the highest proportional increases in 1994; a 99 times increase at site D, and a 47 times increase at site J. Dry peat sites E and G, however, which appeared to have retained enough moisture to allow relatively high numbers of *Tipula subnodicornis* emerge in 1993, did not have such large increases in 1994, suggesting that a mechanism of density-dependence is in operation for *Tipula subnodicornis* on Chapel Fell. This mechanism is not likely to be parasitism or predation as reduction of *Tipula subnodicornis* by these routes have not been found to be large, with Meadow pipit taking <1% of adults available (Coulson & Whittaker, 1978). A more likely density-dependent control of numbers is injury by other larvae, as was observed on Knock Fell (Butterfield,1973).

Though 'dry' peat sites were very variable for *Tipula subnodicornis* totals during 1992 and 1994, a feature of these sites is that even after the 'harsh' spring of 1992, they allowed, in comparison to other sites that year, a relatively large number of this species to survive to adult stage (Table 2). Somehow these dry sites had the capacity to sustain numbers even in poor years, thereby providing a reserve population of *Tipula subnodicornis* to exploit favourable conditions in the following year in the same way that areas of retained water, such as *Sphagnum* flushes, were shown by Coulson (1959) to act as a reservoir from which *Tipula subnodicornis* could repopulate areas after dry spells. In this case, it may be that the 'dry' sites were in actual fact able to retain water more efficiently, or did not dry out as much as the 'wet' sites during dry weather, perhaps due to a thicker layer of soil.

During the spring of 1993, differences between numbers at each dry peat site were small (Fig. 3), yet in the following year, totals were widely different between these sites. These differences in tipulid abundance in 1994 are likely to be due to a combination of site structure and vegetational differences.

That Diptera favour certain species of vegetation within habitat types has been shown for *Culcicoides impunctatus*, a midge which is restricted to wet areas of bogland bearing *Sphagnum* spp. and *Polytrichum* spp., and is absent from marshes and swamps (Kettle, 1952). In tipulids also, variation in density of final instar larvae of *Tipula subnodicornis* was shown to be associated with vegetation type, with densities much higher on *Juncus squarrosus* moorland than on *Sphagnum* bogs (Coulson, 1959). This was indeed the case at site M (dry peat) where high cover of *Juncus squarrosus* (48%) interspersed with *Eriophorum vaginatum* (also favoured by *Tipula subnodicornis* (Coulson, 1962)) corresponded wth very high tipulid numbers, made up of mainly *Tipula subnodicornis* (Fig. 3). The absence of *Juncus squarrosus* at all other peat sites seems a likely explanation for lower numbers of *Tipula subnodicornis* elsewhere.

At mineral A, where *Juncus squrrosus* also gave fairly high cover (25%), numbers of tipulids, due to the paucity of *Tipula subnodicornis*, did not reach high levels - even in comparison to other mineral sites (Fig.2). This suggests that either mineral sites were able to support *Tipula subnodicornis*, but that site A had less favourable soil conditions than the others (C, F, and L) (Fig. 3); or that *T. subnodicornis* at mineral sites was merely due to overspill from other areas, but site A was too far away from *Tipula subnodicornis*' typical peat habitat in order to benefit from this.

At mineral sites, soil moisture levels are relatively low, and it has been suggested by Coulson (1962) that the high mortality in egg and first instar larval stages is caused through dessication. Since then, it has been pointed out by Freeman (1968) that 'as with the larvae, the resistance to dessication of Tipula adults is generally related to the dryness of the environment'.

Low soil moisture levels at mineral sites C and L, however, did not appear to be inhibitory to the presence of *Tipula subnodicornis* with these sites displaying totals comparable to, or greater than those found in areas of much higher soil moisture content. Moreover, site L featured the third highest catch of *Tipula subnodicornis* and tipulids overall. Like site A, this site had *Juncus squarrosus* present and a similar moisture content. In addition, it had a much higher soil organic matter content than all the other mineral sites, which may make this site less prone to dessication. The presence of adult *Tipula subnodicornis,* however, is not necessarily an indication of the location of the habitat for its larvae.

What probably is the most important feature of these sites is that they are close to the main generating areas of *Tipula subnodicornis* (E, M on Map 1). For this reason, fairly high numbers at site C, which had a low organic matter content, may be due to overspill from nearby peat sites. Another possibility at site C, is that *Juncus effusus* closeby to the traps was able to provide a protective habitat from conditions outside of the tufts, as was found with *Tipula paludosa* during daylight (Coulson,1962), thereby sustaining adults in that area. *Tipula subnodicornis* was not prevalent at site C compared to other sites in 1992 or 1993, however, making this an unlikely explanation.

It is important to remember that a 'suitable habitat' refers to both the feeding larval tipulid and also the adult which, during its short existence must find a mate, and, in the case of females, oviposit their eggs (the only feeding requirement for the majority of adult Tipulidae is water). These two requirements amount to the same thing, and it was found by Coulson (1959), that female *Tipula subnodicornis* lay the majority of their eggs close to the point of pupation and of larval life. Accordingly, though larval densities were not looked at in this study - the largest presence of adults would seem a good indication of a habitat that was suitable for development of that species and that, with the right weather conditions, will be suitable for further offspring. In the case of *Tipula subnodicornis* this has been said to be in areas of *Juncus squarrosus* and *Eriophorum vaginatum*, where the presence of suitable food plants such as mosses and liverworts co-exist (Coulson 1962). This agrees with the findings in this study (highest three site totals of *Tipula subnodicornis* = M, L, E), where either, or both of these vegetation species were present. Two of these locations (M & E) are peat sites and so are in accordance with previous studies identifying *Tipula subnodicornis* as a peat-inhabiting species (Coulson, 1959 & 1962) i.e. whiere it completes its lifecycle. Site L, however, is a mineral site, and thus the presence of *Tipula subnodicornis* larvae here is unlikely. Instead, the relatively high numbers of *Tipula subnodicornis* adults here is probably due to large abundance in other peat areas, such as site M, overspilling onto mineral sites, and subsequently, the reason why mineral site A had so few *Tipula subnodicornis* in comparison to other mineral sites is that it was furthest away from peat areas (Map 1).

Apart from on mineral soil, lowest densities are said to occur on *Sphagnum* bog (wet peat) and eroded peat hags (dry peat). The latter was certainly found to be the case at Chapel Fell, with site H barely raising any tipulids.

Trichyphona immaculata is similar to *Tipula subnodicornis* in being described as commonly inhabiting peat (Coulson, 1959) and in this study that is where it was mainly found. In contrast to *Tipula subnodicornis*, however, which decreased at three wet peat sites (D, J & K), and stayed the same at the hag sites, *Trichyphona immaculata* only decreased at one wet peat site (D) in 1994. At site D, numbers of *Trichyphona immaculata* had been depressed so low in 1993, that even with favourable conditions for the next generation of instar development, as shown by site M, recovery did not allow it to reach 1992 levels. Unlike *Tipula subnodicornis*, overspill of *Trichyphona immaculata* onto mineral sites was not greater than the generation of the species on peat sites except site D.

Though soil moisture content measured in July of 1994 was found not to be correlated to tipulid densities as all sites were wet, in other studies it has been found to be a factor with tipulid genera such as *Limnophila* being not normally found away from surface water (Freeman, 1968). Accordingly, bogs have an important ecological feature of always providing available surface water except during prolonged drought.

A difficulty in taking soil moisture readings is choosing the right time for doing so. Soil samples taken this year were after a period of heavy rainfall and thus did not reflect, the 'normal' amounts of soil moisture found at some of the sites. Due to differing drainage/drying characteristics peat soil becomes wetter in comparison to mineral, during, and soon after rain. It is also able to dry quicker, however, and has much 'unavailable' water; as opposed to mineral soil which is able to draw up water from lower levels but at most times will appear drier (Coulson, 1962). In addition to this is the amount of organic content present in soil which has the effect of increasing water holding capacity.

4.3 Tipulid abundance

The large increase in tipulid abundance during 1994 was mainly due to the success of *Tipula subnodicornis* and to a lesser extent *Trichyphona immaculata* as shown in Table 4. Other tipulid species also had more numerous populations in 1994 compared to 1992 and 1993, such as *Limnophila meigeni* and *Molphilus ater*, but these did not contribute large proportions to the total population.

Conditions during early spring of 1994 were cold and wet, inhibiting earlier emergence and development of tipulids, but providing the damp conditions needed for successful larval development preceeding pupation. The requirement for wet habitat conditions is particularly important for first-larval instars of *Tipula subnodicornis, Molophilus ater* and *Trichyphona immaculata* which occur in June and July, and are susceptible to dessication, and rainfall is thus deemed to be important in determining high population densities (Coulson, 1988).

Evidently weather conditions from 1992 to 1993 caused a decline in populations of *Tipula subnodicornis* and *Trichyphona immaculata*, but from 1993 to 1994 allowed a recovery with peat soils retaining enough moisture for survival of larvae through to adult emergence at the end of May 1994 (Appendix I). Population increase of *Tipula subnodicornis,* though, was much more dramatic than for *Trichyphona immaculata* with the former achieving a 19.9 times increase on 1993 figures and the latter managing only an increase of 8.7 times, in 1994. This difference could be a direct effect of their respective fecundities as they appeared to respond to the same environmental cues and were both most successful at the same site (M).

Molophilus ater had the biggest proportional increase with traps yielding 37 times more than the 10 individuals found in Spring 1993. Though its proportion of total tipulids sampled had increased, this was still less than 5%. Hadley (1969) found this species at

Moor House Nature Reserve in the Pennines, to be restricted to areas of blanket bog and where peat is better drained and shallower with *Juncus squarrosus* often dominant. These same conditions also favoured the success of *Tipula subnodicornis* and *Trichyphona immaculata* at Chapel Fell, but these species were more widespread and perhaps able to exploit a wider range of habitats, than *Molophilus ater*. In this study, *Molophilus ater* was found almost exclusively at site M - a site which meets Hadley's descriptions. Two individuals were also found at site A - a mineral soil, but which also dominantly features *Juncus squarrosus*. For the reasons given earlier for *Tipula subnodicornis* being here, however, this was probably due to overspill from other habitats e.g site M. *Molophilus ater* is a decomposer, while most other common tipulids are herbivores (Coulson & Whittaker, 1978). Accordingly, it would be expected to be found in areas where there is a high soil organic content, as was the case at site M.

The third largest contributor to 1994 totals was *Limnophila meigeni* (Table 4). This increased on its numbers compared to previous years, but not on the scale seen with *Tipula subnodicornis* and *Trichyphona immaculata*. Subsequently, compared to these species, it was not common and thus, its percentage of total tipulids decreased significantly, resembling more closely the percentage for 1992. In comparison to the other main contributors to tipulid totals, its numbers have fluctuated the least - even in the 'unfavourable' year of 1993 and irrespective of the general pattern for tipulid totals. It seems this species may be able to succeed in conditions or habitats less beneficial to other species. Although, as earlier mentioned, *Limnophila* species generally require surface water to be available, *Limnophila meigeni* larvae may, perhaps, be more resistant than others during drier years. *Limnophila meigeni* was found to occur mainly on peat sites, but in contrast to the other peat inhabiting species, it was not abundant at site M (Appendix I).

In contrast to all these peat-inhabiting tipulid species, *Tipula varipennis* was found in mostly alluvial areas, with some also occurring at peat site M (Appendix I). This is the same distribution as was described for it by Coulson (1959) at Moor House, but numbers of this species on Chapel Fell in 1994 were very low after having decreased for the third year running.

4.4 Tipulid spring emergence

The main spring emerging species of tipulids - *Tipula subnodicornis, Trichyphona immaculata, Limnophila meigeni, Molophilus ater and Tipula varipennis*; either began to emerge, or at least had their peak abundance, later than in previous years, as demonstrated in Fig. 5. Although 1993 peak abundance figures coincide with those for 1994, 1993 was a much more gradual population increase beginning in early-mid May, largely constituted by *Limnophila meigeni.*

The cause of delayed emergence in tipulids during 1994, was due to diapause as a result of the late arrival of warm spring weather. Insects pupate in response to the stimulus of a marked rise in temperature, usually in late April and May and winter temperatures are said to act as a brake on tipulid development by affecting growth of the fourth, final larval instar (Butterfield, 1976). The timing of emergence is also suggested to be 'related to the annual trend of the water content of the soil during oviposition and possibly at the time of hatching of the eggs' (Coulson, 1962).

Though emergence was delayed in all species, the order of peak emergence did not in every case remain constant. *Limnophila meigeni* retained its two week spacing after peak emergence of *Tipula subnodicornis* and *Trichyphona immaculata*, for its own emergence peak (Fig. 8), but *Molophilus ater* still had its peak abundance coiniciding with 1992 and 1993 (Fig. 9). In previous years, therefore, *Molophilus ater* has had its peak abundance two weeks after *Tipula subnodicornis* and the other main species. This difference in emergence times which is cited as usually being about nine days, however, is said to become less where emergence is late (Coulson *et al.* 1976), and this is what happened on Chapel Fell in 1994.

4.5 Differences relating to use of new and old traps in sampling

The higher success rate of new traps compared to old, in trapping invertebrates, is a trend that was apparent throughout this study, and appears to be another factor for consideration in pitfall trapping, along with those discussed by Luff (1975), Greenslade (1964) and Southwood (1966).

Crititcal studies have warned about the use of pitfall traps and Briggs (1961), in discussing the use of pitfall traps for trapping carabids states 'it is evident that the size of the population plays at most a minor role in determining the numbers trapped', but in this study, they were found satisfactory for trapping tipulids and allowed a method to compare site abundances and record the timing of spring emergence. The location of traps at study sites, however, was not the only factor in affecting numbers of invertebrates caught in them.

In the earlier collections (during April), new traps overall were catching twice as many invertebrates than the old traps, with some invertebrate groups - Araneae, other Diptera - being collected at higher ratios than this (x3 and x3.4 respectively on 15 April), in new : old traps. It is only the Araneae, however, that were collected in high enough numbers to be consistently statistically significant up until 10 June (Table 1).

All groups, examined (except tipulids), demonstrated a general decline in the magnitude of this ratio during subsequent weeks, so that combined, the difference between invertebrates in new and old traps produced the pattern depicted by Fig. 10.

It appears that whatever factor(s) caused the higher numbers of invertebrates found in new traps, decreased with time. The causal factor for higher totals in new traps may either have been something that encouraged invertebrates to enter new traps at a greater rate than those entering old (capture efficiency), or prevented escape more succesfully (retaining efficiency).

To eliminate change in season as being a factor for causing the decline in success of new traps compared to old, brand new traps were re-introduced into the monitoring programme on 10 June. Although new traps generally, continued to represent a significantly higher number of invertebrates on 24 June (Appendix III), brand new traps failed to produce the two-times higher number of invertebrates than captured in old, as would be expected from the ratio on 15 April if 'newness' of trap is the causal factor. Instead they behaved similarly to the new traps which had been in use since 1 April. Any differences in numbers between brand new and nearly new traps that did occur, were inconclusive. Repetition of the experiment on 8 July, but with an extra 13 brand new traps (allowing a comparison of traps with 3 of each type per transect), demonstrated a significantly uneven distribution in favour of brand new traps compared to old, amongst other Diptera and Araneae. With only two out of the fourteen ANOVAs showing significance, however, it should be remembered that a statistically significant result does not necessarily have biological significance.

These results established that the new traps had an advantage over the old, which within the timescale of this experiment was not related to the length of time they had been in the field. It appears that an outside factor such as a change in climate or vegetation growth was somehow influencing this effectiveness. The reason for the decrease in the magnitude of differences between catches in new and old traps was not due to the decay of an innate feature of the new traps, but an interaction with outside influences most likely related to seasonal climate change. One such influence could be a rise in temperatue with the arrival of summer, as correlation between pitfall catches and temperature was found by Briggs (1961) and Greenslade (1961). Temperature may be affecting the outcome either through influencing insect activity directly, or indirectly through influencing trap characteristics. If either of these are the case, then the two times higher invertebrate capture by new traps in April was due to low temperatures having little effect on their relative efficiency.

There are a number of possibilites which could have made new traps more effective in catching invertebrates. Firstly, differences in overhang may be negated as traps were placed in the ground and prepared so that no gap occurred between the mouth rim and surrounding soil. Trap height too, would not be visible to invertebrates as traps were sunk into the ground. Trap height could feasibly have an impact on retaining efficiency, but in this case it was the shorter (new) traps that contained more animals.

Mouth diameter (trap size) has been shown to determine totals of Coleoptera captured in pitfall traps (Luff, 1975), and it is logical that the chance of an animal meeting a trap in its path is proportional to the size of the trap. It is difficult to imagine, though, that an increase of less than 3% in diameter would be responsible for a two times increase of invertebrates overall (15 and 28 April), or a three times increase of invertebrates belonging to a certain group (Araneae, 15 April).

Plastic thickness of the mouth rim is another potential influence on catching efficency and Van der Drift (1951) noted that a carabid (*Notiophilus* sp.) could evade capture by recovering balance on the lip of a pitfall and then escape. Whether such behaviour is aided or made more difficult by a thicker rim is not known, but it is feasible that an increase in vegetational growth with the onset of summer, may have affected this.

Apart from trap dimensions, qualitative differences were also observed between traps in relation to:- colour, odour and texture.

New traps were an opaque (clean) white and thus, more reflective of light than the dull translucent old traps. However, being mostly concealed beneath ground, brightness of new traps is unlikely to have attracted insects in the same way that colour has been reported to be of some importance in trapping the Mexican fruitfly (Baker *et. al.* 1944). Furthermore, experiments by Greenslade (1964), involving camouflaging of traps, and comparisons of white-painted with black and unpainted traps, did not produce variation in catches. Subsequently, the more subtle variation in trap colour involved in this study would not seem to be a likely factor.

This then, leaves trap odour as a possible stimulant causing invertebrates to enter new traps more than old. New traps were observed to have a plastic odour which the old traps did not have. It is possible that this may have acted as a chemo-attractant. Insects that respond to chemo-attractants in nature are predominantly Lepidoptera, Coleoptera and Diptera (Dethier, 1947). Coleoptera and Diptera were common in this study.

In general, classes of attractants either relate to sex, or to food. There are also, however, a few natural odours of doubtful significance e.g. smoke, and unnatural odours which are man-made attractants. Subsequently, observations are recorded of attraction of insects to synthetic compounds which bear no relation to the ecology of the species concerned, e.g. the attraction of kelp flies to the cleaning fluid trichlorethylene (Williams, 1943). A chemopositive response by invertebrates to plastic odour is then, a credible possibility, and this could conceivably be affected by temperature and humidity as a result of seasonal climate change. In this case trap odour, may somehow have been more effective in April as a result of the lower average temperature then.

The final qualitative difference between traps to consider is texture. New traps had a smooth, clean inner surface, whilst old traps had a rougher, grimed surface. It has been observed that plastic pitfall traps can allow Coleoptera to escape with escape rates calculated to be about 4% a day, in comparison to 10% from metal traps and neglible losses from glass traps (Luff, 1975). It has further been suggested by Luff (1975) that 'plastic and metal traps may allow even easier escape when they are dirty'. Preservatives, such as formalin, as was used in traps in this study, should prevent such loss, but Petruska (1969) showed that small Carabidae could escape from formalin-filled traps and that Staphylinidae of all sizes were able to escape. This highlights the fact that smoothness of sides may affect retaining efficiency even in traps containing formalin. The differences between catch rates in new and old traps in this study, however, were far more than even the biggest difference between glass and metal traps (10%) discovered by Luff (1975).

A curious anomaly to this trend of more invertebrates in new pots was presented by tipulids. These, contrary to other groups, tended to occur more in old traps at highly significant levels on 27 May ($F=_{(1,104)}8.06; P<0.01$), and 10 June ($F=_{(104)}7.09; P<0.01$) than in new. Furthermore, in a reversal of the situation for all other invertebrates, this difference decreased with time, so that tipulid numbers in old traps on the second date of sampling (10 June), became closer to unity with new traps. It would seem, that whatever factor was an attractant to other invertebrate groups, was a repellant to the tipulids. This idea is made even more convincing by the large decrease in ratio (2.5 to 1.1 in favour of old) two weeks later, i.e. the decrease in the strength of the factor possessed by new traps that was an attractant to other invertebrates, spelt a decrease in its repellency to tipulids.

The fact that tipulids (at least during peak emergence) were caught more in old traps, suggests that texture of trap sides was not the influencing factor. Trap odour acting as chemical stimulant seems a likely cause for the differences observed. In the case of most invertebtates, this chemical stimulant was an attractant, but for tipulids it was a repellent - a substance which elicits an avoiding reaction in organisms.

Experiments with European vine moths have shown that the degree of attraction increases with concentration of the chemical stimulus (Luff,1975). It is also the case, however, that at higher concentrations an attractant chemical may become a repellant. Moreover, 'most odours are repellent if their concentration is great enough' (Dethier, 1947). It may well be then, that the odour from new traps, an attractant for most invertebrates, was above a threshold concentration for male tipulids, which in their non-feeding adult stage are sensitive to female pheremones. This would seem especially likely in the knowledge that in contrast to attractants which can be species-specific, repellents are non-specific in their action (Dethier, 1947), and therefore, if plastic odour was repellent to tipulids, it would presumably be repellent to other invertebrates as well.

The impact of these results is that they demonstrate how traps may give differing results which have nothing to do with the location and natural ecology of the habitat in which they are situated. Apart from keeping traps standard in size and shape, it is important that their age is considered also. Greenslade (1964), in his analysis of pitfall trapping

Coleoptera states: 'pitfall traps must be used with discretion, especially for comparative purposes'.

With these dangers in mind, pitfall traps may still be considered 'useful as a collecting device' (Southwood, 1975), though there is uncertainty as to how representative their results may be of an areas' invertebrate fauna. In their favour however, they allow a method of study for seasonal incidence and comparison of habitats which requires little maintenance and cost, as was the case in this study.

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Appendix I. Table of abundance for the major tipulid species on Chapel Fell at individual study sites during May to July, 1994.

	A	B	C	D	E	F	G	H	J	K	L	M	N	P	**Total**
Tipula subnodicornis	52	172	382	198	436	239	197	12	279	200	506	2496	10	3	5182
Trichyphona immaculata	45	99	34	46	96	28	60	20	109	201	57	580	23	0	1396
Limnophila meigeni	0	117	16	30	84	4	129	1	62	56	3	4	6	2	514
Molophilus ater	2	0	0	0	0	0	0	0	0	0	0	368	0	0	370
Ormosia pseudosimilis	58	0	27	24	0	9	1	0	1	0	0	40	0	0	160
Tipula varipennis	16	0	3	1	0	0	0	0	0	0	6	9	0	0	35

Appendix II. Soil moisture content at study sites A - M on Chapel Fell - recorded in mid July, 1992

Site	A	B	C	D	E	F	G	H	J	K	L	M
% Moisture	27	84	30	80	85	32	79	66	75	75	48	77

Appendix III. Totals of grouped invertebrates occurring in New and Old pitfall traps, from April to July, 1994.

Collection		15 April	28 April	13 May	27 May	10 June		24 June	8 July
TIPULIDS	BN	0	0	0	31	2641	BN	254	66
	Old	0	0	0	79	3008	NN	303	63
							Old	262	52
OTHER DIPTERA	BN	24	105	218	533	1565	BN	218	283
	Old	7	56	165	415	1272	NN	244	199
							Old	162	201
DIPTERA LARVAE	BN	79	87	27	17	24	BN	18	23
	Old	53	31	11	8	14	NN	15	25
							Old	4	22
ARANEAE	BN	102	497	288	376	1068	BN	811	623
	Old	34	224	184	248	676	NN	825	446
							Old	492	411
CARABIDS	BN	4	66	175	111	342	BN	101	258
	Old	2	54	135	96	209	NN	141	230
							Old	96	236
STAPHYLINIDS	BN	7	37	59	36	199	BN	62	264
	Old	3	38	47	28	138	NN	46	258
							Old	38	126
COLEOPTERA LARVAE	BN	5	12	12	13	33	BN	19	41
	Old	5	6	8	7	29	NN	15	39
							Old	11	32
TOTAL INVERTS	BN	229	936	881	1205	5448	BN	1621	1806
	Old	117	479	658	980	5030	NN	1683	1505
							Old	1124	1356

BN = brand new traps
NN = nearly new traps (used in the field since 1 April)
Old = old traps (used in the field for a number of years)

nb. These figures do not represent total captures at each site, as not all traps used for sampling were considered for comparison of trap type.